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Minimal standards for describing new species belonging to the families *Campylobacteraceae* and *Helicobacteraceae*: *Campylobacter, Arcobacter, Helicobacter* and *Wolinella* spp.

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Abstract

Ongoing changes in taxonomic methods, and in the rapid development of the taxonomic structure of species assigned to the Epsilonproteobacteria have lead the International Committee of Systematic Bacteriology Subcommittee on the Taxonomy of *Campylobacter* and Related Bacteria to discuss significant updates to previous minimal standards for describing new species of *Campylobacteraceae* and *Helicobacteraceae*. This paper is the result of these discussions and proposes minimum requirements for the description of new species belonging to the families *Campylobacteraceae* and *Helicobacteraceae,* thus including species in *Campylobacter, Arcobacter, Helicobacter,* and *Wolinella.* The core underlying principle remains the use of appropriate phenotypic and genotypic methods to characterise strains sufficiently so as to effectively and unambiguously determine their taxonomic position in these families, and provide adequate means by which the new taxon can be distinguished from extant species and subspecies. This polyphasic taxonomic approach demands the use of appropriate reference data for comparison to ensure the novelty of proposed new taxa, and the recommended study of at least five strains to enable species diversity to be assessed. Methodological approaches for phenotypic and genotypic (including whole-genome sequence comparisons) characterisation are recommended.

INTRODUCTION

The class Epsilonproteobacteria is a phylogenetically-distinct lineage within the Proteobacteria [1] and currently contains 16 genera (Tables S1 and S2, available with the online version of this article). The genus *Campylobacter* was the first of these established [2], and the realisation that certain species were important human and animal pathogens prompted many further studies investigating the wider ecology and distribution of similar organisms. Bacteria found in cases of human gastritis and initially classified as *Campylobacter* spp. were later reclassified into a separate but related genus, *Helicobacter* [3]. Improvements in isolation, detection and taxonomic characterization methods, together with continued interest in the significance and distribution of such bacteria have resulted in the present status of the Epsilonproteobacteria – a highly diverse group of organisms containing over 100 taxa.

Within the class, phylogenetic subgroups can be identified. Of these, most taxa in the families *Campylobacteraceae* (namely *Campylobacter, Arcobacter* and *Sulfurospirillum)* and *Helicobacteraceae* (namely *Helicobacter* and *Wolinella*) appear more closely related to each other than to free-living Epsilonproteobacteria such as the Nautiliaceae [4]. Their known or potential significance as pathogens, and advances in cultivation, make *Campylobacter* and *Helicobacter* the most populous genera, with many taxa sharing the same ecological niche. Their close phenotypic similarity to each other is illustrated by many *Arcobacter, Sulfurospirillum* and *Helicobacter* spp. having originally been described as '*Campylobacter*' species (reviewed in [5]).

In every year since 1988, at least one novel species belonging to at least one of these genera has been described. On occasion, descriptions have been controversial [6–9], and on several occasions the ICSP Subcommittee on the Taxonomy of *Campylobacter* and Related Bacteria have remarked on the sometimes questionable quality of particular species descriptions that were observed [10–12]. Furthermore, taxonomic methods have undergone a 'sea change' with whole-

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Keywords: minimal standards; species descriptions; polyphasic taxonomy; *Campylobacteraceae*; *Helicobacteraceae*; *Arcobacter*; *Wolinella*; Epsilonproteobacteria.
Abbreviations: ANI, average nucleotide identity; GBDP, Genome Blast Distance Phylogeny; TMAO, trimethylamine N-oxide.
Two supplementary tables are available with the online version of this article.

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genome sequencing offering a new and more detailed perspective on organismal relationships.

This paper accounts for these substantive changes and expands and updates previously-published minimal standards for describing new species of *Campylobacteraceae* [13] and *Helicobacter* [14]. Table S1 lists the current, validly-described species names in the genera covered by this proposal with their type strains and accompanying 16S rRNA gene sequence accession number. Members of the genus *Sulfurospirillum* are exclusively free-living and, from an ecological perspective, have more in common with, for example, members of the *Nautilaceae* (cf. Table S2), for which minimal standards will be proposed in due course. Intriguingly, phylogenetic analyses based on both 16S rRNA gene sequences (Fig. 1), and concatenated protein sequences derived from a subset of 289 conserved single-copy-number genes reveal a close relationship between *Sulfurospirillum* and *Campylobacter* [15], despite these taxa inhabiting radically different ecological niches. Such observations highlight the complexities of the Epsilonproteobacteria group as a whole, and support the need for a polyphasic taxonomic approach for accurate classification.

GENERAL FEATURES OF *CAMPYLOBACTERACEAE*

Gram-negative, curved, spiral or occasionally straight rod-shaped cells, 0.2–5 µm long. Cells may become more spherical after time or with exposure to environmental stress. Non-spore forming. Most species are motile by use of one to two unsheathed polar flagella, but a few species are aflagellate. Optimum growth temperatures range from 25 °C (notably *Arcobacter* spp.) to 42 °C (some *Campylobacter* spp.). All *Campylobacter* spp. can be cultured at 37 °C under appropriate conditions. The optimal growth atmosphere for *Campylobacteraceae* is microaerobic – traditionally, such atmospheres are described as comprising 3–8 % O_2, with commonly available Gaspak systems providing the balance with 10 % CO_2 and the remainder as N_2. However, some species require H_2 for growth and studies have demonstrated all *Campylobacter* spp. can grow in an atmosphere of 3 % O_2, 7 % H_2, 10 % CO_2 and 80% N_2. Most *Arcobacter spp.* demonstrate the ability to grow under aerobic conditions (*A. anaerophilus* is an exception as an obligate anaerobe) [16], but all arcobacters to date can grow at 20–30 °C. Most species produce oxidase (undetected in *C. gracilis* and in some strains of *C. showae* [17]) and, in conventional laboratory testing for oxidation and/or fermentation of glucose, (e.g. [18]), do not demonstrate the ability to ferment or oxidise carbohydrates. *Campylobacter* and some *Arcobacter* spp. may be associated with the oral environment and/or the enteric or reproductive tracts of host animals; some *Arcobacter* spp. are free-living [4, 5, 16].

GENERAL FEATURES OF *HELICOBACTERACEAE*

Gram-negative, spiral, helical, curved, or fusiform rods of width 0.3–0.6 µm and length 1–5 µm. Cells may become more spherical after time or with exposure to environmental stress. Non-spore forming. Most species are motile by means of single or multiple flagella. In most species the flagella are sheathed. Optimum temperatures of growth range from 37 to 42 °C and all known species can be cultured at 37 °C. They are usually microaerophilic and best cultured in atmospheres containing H_2. Oxidase producing with most strains producing catalase. Gastric *Helicobacter* spp. described to date predominantly produce copious amounts of urease. Using common laboratory methods (e.g. [18]), *Helicobacteraceae* do not demonstrate the ability to ferment or oxidise carbohydrates. *Helicobacter* and *Wolinella* species described thus far have been associated with gastric, enteric, reproductive and/or hepatic environments of a variety of host animal species [1, 3, 7, 14, 19, 20]; none are known to be free-living.

General comments

The description of new species belonging to *Campylobacteraceae or Helicobacteraceae* should be based on characteristics necessary for assigning the new taxon to the genus, and on characteristics serving to differentiate the new taxon from existing taxa of the genus. In practice, this will require a polyphasic taxonomic approach utilizing both genotypic and phenotypic methods, especially since there is no single phenotypic characteristic that readily enables the assignation of strains to the genera *Campylobacter, Arcobacter, Helicobacter* or *Wolinella*. Furthermore, species such as *C. coli* and *H. pullorum* may be found in the same environments (presently chickens and humans) and share many phenotypic characters, rendering them difficult to discriminate using conventional phenotyping [5]. Thus, a phylogenetic assignation based on, at least, comparative analysis of 16S rRNA gene sequences is mandatory to appropriately assign strains to genus level [5, 21]. Corresponding sequences from type strains of relevant, validly-named Epsilonproteobacterial taxa should be included in sequence comparisons to appropriately designate phylogeny and thus genus placement. Additional gene sequence comparisons, such as *atpA* [22], *rpoB* [23] or *groEL* (Hsp60) [24], may provide useful information for strain classification and a finer resolution of taxonomic identity.

The description should ideally be based on not fewer than five isolates from different sources, or five distinct genotypes (i.e. representing distinguishable, individual strains) from the same or similar sources. The most useful taxonomic descriptions involve studies where species heterogeneity can be adequately assessed.

For critical comparisons with other species, controls consisting of type or reference strains of the appropriate taxa must be tested. For all phenotypic test procedures, the inoculum size, composition of the gaseous atmosphere,

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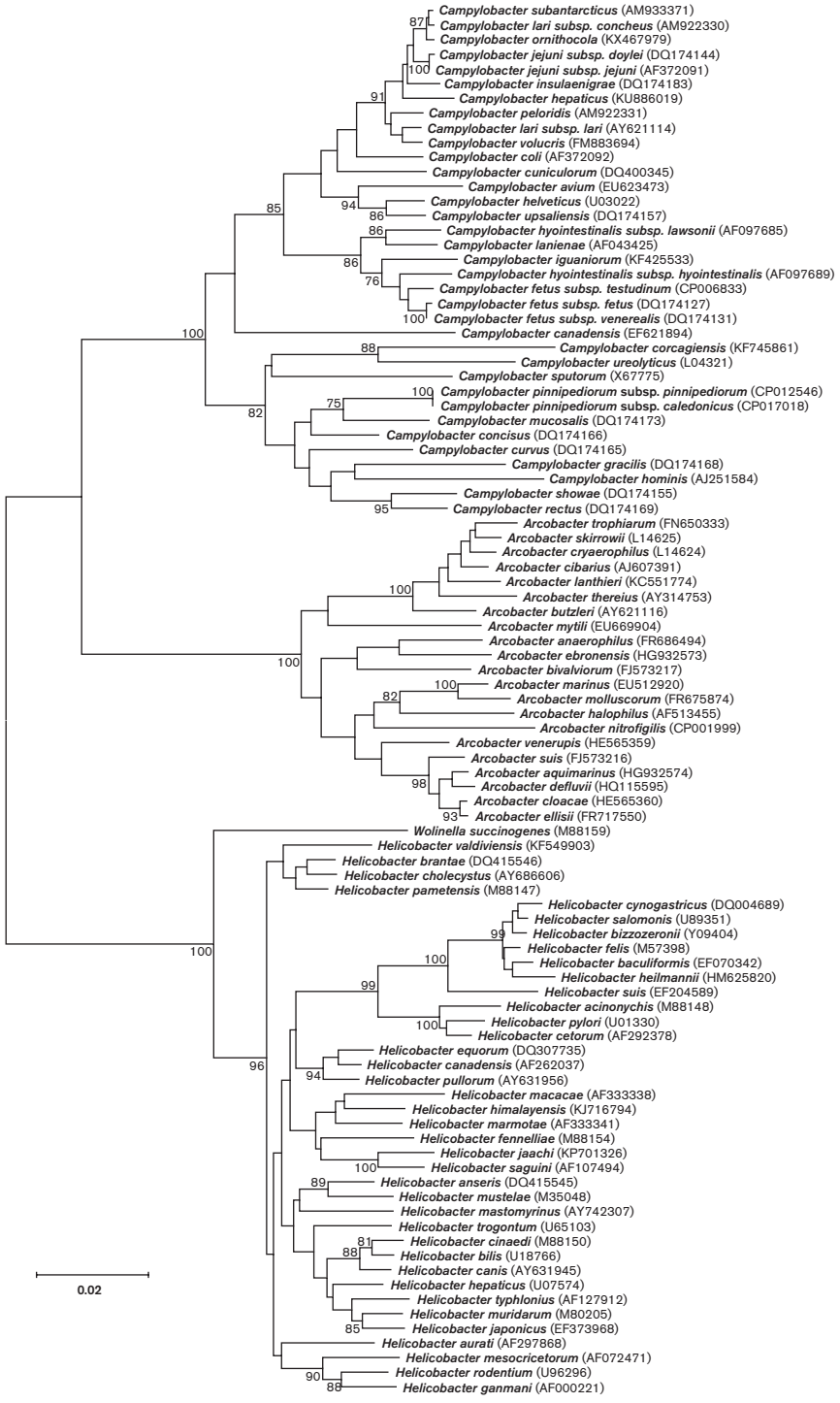

Fig. 1. Phylogenetic relationships between 16S rRNA genes of type strains of the taxa encompassed in this study inferred by neighbor-joining tree using the Kimura 2-parameter distance estimation method, with bootstrapping based on 500 replicates.

temperature and period of incubation, and composition of the basal growth medium should be stated. The use of standardized, well-described tests and methods is recommended to facilitate comparison [25–29]. For descriptions at the species level, the use of advanced phenotypic methods, such as and including MALDI-TOF MS analysis, should be regarded as supportive data but not the primary means by which species are delineated at the phenotypic level. Present

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studies, although limited to relatively few taxa, indicate this approach has promise [30–33] with some caveats [34].

Putative new species of uncultured organisms for which molecular sequence data (such as 16S rRNA sequence) is available may qualify for assignment to the provisional taxonomic status *Candidatus* [35] in accordance with the proposals of Murray and Stackebrandt [36], as exemplified by the initial description of *C. hominis* prior to its culture [37].

Cell morphology

The reaction of cells in the Gram-staining procedure must be stated. The shape, size, and spiral wavelength (where appropriate) of bacterial cells should be reported. The tendency to undergo transformation to coccoid forms on exposure to air or in older cultures should be noted and the time taken for cells to change their appearance provided. The number and arrangement of flagella should be determined by electron microscopy, as well as the presence or absence of flagellar sheaths and periplasmic fibers.

Motility

Cells should be observed by microscopic examination of wet mounts or hanging drop preparations of young cultures in buffered saline or broth.

Growth conditions

Factors affecting growth should be tested under conditions that are near optimal unless stated otherwise.

(1) Colony morphology. The size, shape, and colour of colonies should be described for optimal growth conditions on solid media. The type of nutrient agar base medium used (brain-heart infusion [BHI], Mueller-Hinton etc.) and the manufacturer from which it was obtained should be stated. The presence of swarming on solid media should be noted. When cultured on blood-containing agar media, the percentage and species of blood (e.g. horse, sheep, cattle) should be stated and any haemolytic activity described.
(2) Temperature range. The time of incubation and ability to grow in specified broth or agar media from standardized inocula at various temperatures should be reported. The following temperatures should be used: 25, 37 and 42 °C.
(3) Gaseous requirements. The ability of the strains to grow under aerobic, microaerobic and anaerobic conditions should be reported. The oxygen and hydrogen content must be specified for microaerobic conditions. The means by which such conditions were produced (e.g., gas replacement method, commercial gas-generating sachet [state manufacturer], incubator) must be given.

Biochemical properties

Results for the following tests are required: (i) oxidase activity, by use of any conventional method [28]; (ii) catalase activity, with percentage of reagent solution and time of observation given; (iii) nitrate reduction, preferably by the plate method of Cook [38]; (iv) indoxyl acetate hydrolysis, preferably using a disc method [28] with percentage of reagent solution, volume of impregnation and time of observation given; (v) urease activity, using a rapid method [39]; (vi) alkaline phosphatase activity [40], with time of observation given; (vii) hippurate hydrolysis [41]; and (viii) selenite reduction [28]. Growth on media containing the following compounds using standardized methods [26, 27] should be determined: 2.0 % NaCl, 1 % glycine and 0.04 % triphenyl tetrazolium chloride (TTC): the ability of strains to reduce the latter should also be recorded when growth is observed.

Other tests

Test results for the following are desirable: γ-glutamyl transpeptidase [25]; growth on media containing 3.5 % NaCl, 0.032 % methyl orange, and 0.1 % sodium fluoride [26, 27, 29]; and anaerobic growth on 0.1 % trimethylamine N-oxide (TMAO) [27].

Resistance to antimicrobial agents

Susceptibility to nalidixic acid (30 μg) and cephalothin (30 μg), should be determined either by disc-diffusion or plate MIC tests. For diffusion assays, the absence of a clear zone of inhibition should be recorded as resistance; for susceptible strains, the inhibition zone sizes should be stated. The type of base medium used should be stated. Mueller-Hinton agar with added 10 % horse – or sheep – blood is recommended. Standardised procedures should be employed [26, 27, 42]. Brucella Agar and other media with bisulfite have been shown to inhibit the growth of *H. pylori* and therefore should be avoided [43].

Summary Tables for recommended phenotypic tests for *Arcobacter, Campylobacter, Helicobacter* and *Wolinella* spp. are provided (Tables 1, 2 and 3).

Phylogenetic analyses

The essentially complete (greater than 1450 bases) 16S rRNA sequence must be determined for the type strain, and ideally at least four additional independent isolates of the putative new species or subspecies. Specific methods for sequencing 16S rRNA from *Helicobacter* species, including intervening sequences (IVS), have been described [44]. Intervening sequences in the 16S rRNA gene should be fully sequenced and the 16S rRNA gene sequence, including any IVS, deposited in nucleic acid databases as a single sequence. Deposition of a complete genome sequence accomplishes this goal de facto. The phylogenetic position of representative strains of the putative new taxon must be determined by comparative sequence analysis of the 16S rRNA macromolecule [21]. Phylogenetic tree construction should demonstrate that the novel sequence clusters with those of all validly-named taxa of the appropriate genus within the *Campylobacteraceae* or *Helicobacteraceae*. A full description of alignment and treeing methods, including software, algorithms, treatment of gap penalties, and treatment of IVS sequences should be included. An exemplar tree is presented in Fig. 1.

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Table 1. Summary phenotypic data for extant *Arcobacter* spp.

Data are derived from original species descriptions [16, 50, 74–88] (cf. Table S1) and/or On *et al.* [17].

	1	2	3	4	5	6	7	8	9	10
Growth temperature range (°C)	18–37	18–37	18–37	18–37	18–37	18–37	18–25,[37, 42]	18–37,42*	18–30	18–37, 42†±
Atmospheric requirements	ANO2	O2, mO2, ANO2†	O2, mO2, ANO2	O2, mO2, ANO2	[O2], mO2, ANO2*	O2, mO2	O2, mO2, [ANO2]	O2, mO2, ANO2†	O2, mO2	O2, mO2, ANO2±
Oxidase	−	+	+	+	+	+	+	+	+	+
Catalase	−	+	+	V	V	+	+	±	−	+
Nitrate reduction	+	+	−	+	−	+	V	+	−	+
Indoxyl acetate hydrolysis	+	+	+	+	+	+	+	+	+	+
Urease	−	−	−	−	−	−	−	+	+	V
Alkaline phosphatase	U	U	U	−	−	U	−	U	U	U
Hippuricase	U	U	U	−	−	U	−	U	U	U
Selenite reduction	U	U	U	−	−	U	−	U	U	U
Growth on: 2 % NaCl	+	+	+	M	−	+	M	+	+	+
1 % glycine	+	−	−	−	−	−	−	−	−	−
0.04 % TTC	−	−	−	+	V	+	M	−	−	−
TTC reduction	−	−	−	+	−	U	M	−	−	−
Resistance to: Nalidixic acid (30 mg)	U	U	U	F	V	U	−	U	U	U
Cephalothin (30 mg)	U	U	U	+	+	U	+	U	U	U
Desirable features:										
g-glutamyl transpeptidase	U	U	U	U	U	U	U	U	U	U
Growth on:										
3.5 % NaCl	+	U	+	V	−	+	−	U	+	U
0.032 % methyl orange	U	U	U	+	+	U	+	U	U	U
0.1 % sodium fluoride	U	U	U	+	V	U	+	U	U	U
Anaerobic growth on 0.1 % TMAO	U	U	U	+	±	U	F	U	U	U

	11	12	13	14	15	16	17	18	19	20	21
Growth temperature range (°C)	18–37	25–37	10–40	18–37,42±*	18–37,42±†	18–25	18–37,[42]	18–30	18–30	18–30	18–37
Atmospheric requirements	O2, mO2, ANO2	O2, mO2	O2, mO2	O2, mO2, ANO2±	O2, mO2, ANO2†	O2, mO2, ANO2	O2, mO2, ANO2	O2, mO2	O2, mO2	O2, mO2	O2, mO2
Oxidase	+	+	+	+	+	+	+	+	+	+	1
Catalase	−	+	−	+	+	+	+	+	+	+	1
Nitrate reduction	+	+	+	+	+	+	+	+	+	−	1
Indoxyl acetate hydrolysis	+	+	+	−	−	+	+	+	+	+	1
Urease	−	U	−	−	−	+	−	−	−	−	1
Alkaline phosphatase	−	−	−	U	+	−	−	U	−	U	U
Hippuricase	−	−	−	U	U	−	−	U	−	−	U
Selenite reduction	−	U	U	U	U	V	F	U	−	+	U

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Table 1. cont.

	11	12	13	14	15	16	17	18	19	20	21
Growth on: 2 % NaCl	+	U	+	+	+	+	+	–	M	V	1
1 % glycine	–	+	+	–	+	–	–	–	+	–	–
0.04 % TTC	–	U	–	–	–	–	+	–	V	–	–
TTC reduction	–	+	–	–	+	–	+	–	V	–	–
Resistance to: Nalidixic acid (30 mg)	–	–	U	U	U	–	–	U	V	U	U
Cephalothin (30 mg)	–	U	U	U	U	–	+	U	+	+	U
Desirable features:											
g-glutamyl transpeptidase	U	–	U	U	U	U	U	U	U	U	U
Growth on:											
3.5 % NaCl	+	U	+	+	+	+	+	–	V	V	+
0.032 % methyl orange	–	U	U	U	U	+	+	U	+	U	U
0.1 % sodium fluoride	–	U	U	U	U	+	+	U	+	U	U
Anaerobic growth on 0.1 % TMAO	U	U	U	U	U	+	–	U	V	U	U

1, *A. anaerophilus*; 2, *A. aquimarinus*; 3, *A. bivalviorum*; 4, *A. butzleri*; 5, *A. cibarius*; 6, *A. cloacae*; 7, *A. cryaerophilus*; 8, *A. defluvii*; 9, *A. ebronensis*; 10, *A. ellisii*; 11, *A. halophilus*; 12, *A. lanthieri*; 13, *A. marinus*; 14, *A. molluscorum*; 15, *A. mytili*; 16, *A. nitrofigilis*; 17, *A. skirrowii*; 18, *A. suis*; 19, *A. thereius*; 20, *A. trophiarum*; 21, *A. venerupis*. +=all strains examined give a positive result. –=all strains examined give a negative result. O2, aerobic conditions; mO2, microaerobic conditions; ANO2, anaerobic conditions. ()=variable (31–58 %) number of strains grow at this temperature; []=few (11–25 %) strains grow in these conditions; V, 33–67 % strains positive; ±, weak activity; †=O2 only; †, at 30 °C only; F, 22–25 % strains positive; M, 84–95 % strains positive. U, unknown at this time.

The 16S rRNA gene is the most widely used phylogenetic marker but there are known problems with the accurate phylogenetic placement of certain species within the *Campylobacteraceae* or *Helicobacteraceae* [7, 45–47]. The use of additional phylogenetic markers such as *atpA* [22], *rpoB* [23] or *groEL* [24], may provide useful data to support the phylogenetic position of the new taxon. Multi-Locus Sequence Analysis [48] or rMLST [49] may provide a more robust description of the taxonomic position of a given strain. Taxonomic studies of *Campylobacteraceae* or *Helicobacteraceae* species using MLSA and rMLST are as yet uncommon, although MLSA has been applied to *Arcobacter* species [32, 50]. Ultimately, these approaches can be expected to be replaced by whole genome sequence based phylogenomic analyses (e.g. [15, 51, 52]). As with 16S rRNA gene sequence comparisons, representatives of all extant validly-published named taxa in the genus in which the proposed novel organism is placed must be included.

Genomic analyses

A complete genome sequence of the proposed type strain of a novel species or subspecies is a definitive means to determine the guanosine-plus-cytosine (% G+C) content of the DNA; however, classical methods (melting temperature or enzymatic) may also be used [53]. Reference DNA such as *Escherichia coli* ATCC 11775^T (G+C, 51 mol%) or *H. pylori* ATCC 700392 (G+C, 39 mol%) should be analysed at the same time and its estimated G+C content (moles percent) expressed relative to the reference DNA should be reported.

The current taxonomic definition of a species requires determination of the whole-genomic similarity, whereby at or around 70 % DNA–DNA relatedness indicates strains are sufficiently related to be assigned to the same species [54–56]. Methodological caveats notwithstanding (discussed below), novel species should demonstrate genomic relatedness to extant species at values discernibly lower than this level. The proposed type strain for any new taxon must be used in these comparisons.

Whole-genome relatedness can be tested in several ways. Classical DNA–DNA hybridization experiments have been used for many years (e.g. [57–60]). It is recognized that experiments on Epsilonproteobacteria can be difficult and that different methods can result in differing estimates of the degree of relatedness between strains [61, 62]. Numerical comparison of whole-cell protein profiles [5, 6, 60], and high-resolution amplified fragment length polymorphism (AFLP)-based fingerprints has also been shown to be effective in accurately determining genetic relationships between strains [63, 64]. It is essential that analyses are performed against a database of strain profiles of sufficient number and quality that represent all taxa with validly described species names, for results to be meaningful.

Where whole-genome sequences of proposed new species are available, *in silico* analyses that mimic conventional DNA–DNA hybridisations can be used in comparisons with type strain genomes of validly-published extant species,

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Table 2. Summary phenotypic data for extant *Campylobacter* spp.

Data are derived from original species descriptions [6, 31, 60, 67–69, 87–120] (cf. Table S1) and/or On *et al.* [17].

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Growth temperature range (°C)	37–42	37–42	30–42	(30), 37, (42)	25–42	37, (42)	30, 37, (42)	(18–22), 25–37, (42)	25–37, (42)	<18–22>, (25), 37	(30), 37, (42)	37–42	[30], 37–42	37	[18–25], 30–42	30–42
Atmospheric requirements	mO2	mO2, ANO2	mO2	HmO2, ANO2	ANO2, mO2*	mO2	ANO2, [HmO2]	mO2, [ANO2]	mO2, ANO2	mO2, (ANO2)	ANO2, [HmO2]	mO2	mO2	ANO2, [HmO2]	Mo2	mO2, ANO2
Oxidase	+	+	+	V	+	+	+	+	+	+	−	+	+	+	+	+
Catalase	+	V	+	−	+	+	−	+	+	+	V	+	−	−	+	+
Nitrate reduction	+	V	+	F	M	+	+	+	+	M	M	V	+	V	+	+
Indoxyl acetate hydrolysis	+	−	+	−	V	+	V	−	−	−	M	+	+	−	−	−
Urease	−	V	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Alkaline phosphatase	U	−	−	M	+	−	V	−	−	−	−	U	−	−	−	F
Hippuricase	+	−	−	−	−	−	F	−	−	−	−	M	−	−	−	−
Selenite reduction	U	U	+	F	U	−	−	M	U	F	−	U	−	−	+	+
Growth on: 2% NaCl	U	−	−	F	+	−	V	−	U	−	V	_	F	U	−	−
1% glycine	+	V	M	F	+	−	+	+	+	F	+	+	V	+	+	V
0.04% TTC	U	U	+	−	−	V	+	−	+	−	−	+	−	−	F	−
TTC reduction	U	U	+	−	−	V	V	−	+	−	−	U	−	−	F	−
Resistance to: Nalidixic acid (30 mg)	−	V	−	M	+	V	+	+	U	V	V	+/i	−	V	+	+
Cephalothin (30 mg)	+	−	+	−	−	M	−	−	U	−	−	M	−	−	F	−
Desirable features:																
g-glutamyl transpeptidase	−	+	U	U	U	−	U	U	U	U	U	U	U	U	U	U
Growth on:																
3.5% NaCl	U	−	−	−	U	−	−	−	−	−	−	−	−	U	−	−
0.032% methyl orange	U	U	+	M	U	U	V	+	U	M	V	U	V	U	+	+
0.1% sodium fluoride	U	U	+	M	U	U	−	M	U	M	M	U	−	+	V	−
Anaerobic growth on 0.1% TMAO	U	U	−	M	U	U	+	F	U	F	+	U	−	+	M	M

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Growth temperature range (°C)	18–37	37	37	(30), 37-42	37–42	37–42	30–42	30–42	37–42	37–42	37	37	<30>, 37, <42>	30–37, [42]	(30), 37, [42]	37–42	30–37, [42]	30–37, [42]	37–42
Atmospheric requirements	mO2, ANO2*	mO2	mO2	mO2	mO2, ANO2*	mO2	mO2	mO2, ANO2	mO2, ANO2	mO2	mO2, ANO2	mO2, ANO2	ANO2, [HmO2]	ANO2, [HmO2]	mO2,ANO2	mO2, ANO2	mO2	ANO2, [HmO2]	mO2, ANO2*
Oxidase	+	+	+	+	+	+	+	+	−	+	+	+	+	V	+	+	+	+	+
Catalase	+	+	M	+	+	+	+	−	+	+	+	−	F	V	V†	+	−	F	+
Nitrate reduction	+	+	−	+	+	+	+	F	V	U	+	+	+	+	M	+	+	+	+
Indoxyl acetate hydrolysis	−	−	+	M	−	U	F	−	−	U	−	−	+	V	−	−	+	F	−
Urease	−	−	−	−	−	−	V§	−	+	U	−	−	−	−	V‡	−	−	+	−

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Table 2. cont.

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Alkaline phosphatase	U	U	–	–	+	U	–	M	–	U	U	U	–	–	–		–	–	–
Hippuricase	–	–	+	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Selenite reduction	U	+	–	M	U	U	V	F	U	U	U	U	–	–	V	–	+	–	+
Growth on: 2 % NaCl	U	–	–	–	U	+	M	M	U	M	U	U	V	+	+	+	–	+	–
1 % glycine	+	+	F	M	–	+	+	V	+	+	–	–	+	V	+	M	+	+	–
0.04 % TTC	U	+	V	M	U	U	M	–	U	U	U	U	–	–	–	U	V	–	–
TTC reduction	U	+	V	M	U	U	M	–	F	U	U	U	–	–	–	U	V	–	–
Resistance to: Nalidixic acid (30 mg)	+	+	–	–	+	–	V	M	U	M	–	–	M	–	M	+	–	–	+
Cephalothin (30 mg)	–	+	–	M	+	+	+	F	U	F	–	–	–	–	–	–	F	–	+
Desirable features:																			
g-glutamyl transpeptidase	+	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
Growth on:																			
3.5 % NaCl	U	–	–	–	U		–	–	U	U	U	U	–	–	V	–	–	+	–
0.032 % methyl orange	U	–	+	+	U	U	+	+	U	U	U	U	–	–	+	U	+	+	+
0.1 % sodium fluoride	U	–	F	+	U	U	+	–	U	U	U	U	–	+	M	+	–	+	+
Anaerobic growth on 0.1 % TMAO	U	V	–	–	U	U	+	+	U	U	U	U	+	V	M	+	–	+	U

1, *Campylobacter avium;* 2, 3, *Campylobacter coli;* 4, *Campylobacter concisus;* 5, *Campylobacter corcagiensis;* 6, *Campylobacter cuniculorum;* 7, *Campylobacter curvus;* 8, *Campylobacter fetus* subsp. *fetus;* 9, *Campylobacter fetus* subsp. *testudinum;* 10, *Campylobacter fetus* subsp. *venerealis;* 11, *Campylobacter gracilis;* 12, *Campylobacter hepaticus;* 13, *Campylobacter helveticus;* 14, *Campylobacter hominis;* 15, *Campylobacter hyointestinalis* subsp. *hyointestinalis;* 16, *Campylobacter hyointestinalis* subsp. *lawsonii;* 17, *Campylobacter iguaniorum;* 18, *Campylobacter insulaenigrae;* 19, *Campylobacter jejuni* subsp. *doylei;* 20, *Campylobacter jejuni* subsp. *jejuni;* 21, *Campylobacter lanienae;* 22, *Campylobacter lari* subsp. *concheus;* 23, *Campylobacter lari* subsp. *lari;* 24, *Campylobacter mucosalis;* 25, *Campylobacter ornithocola,* 26, *Campylobacter peloridis;* 27, *Campylobacter pinnipediorum* subsp. *pinnipediorum;* 28, *Campylobacter pinnipediorum* subsp. *caledonicus;* 29, *Campylobacter rectus;* 30, *Campylobacter showae;* 31, *Campylobacter sputorum;* 32, *Campylobacter subantarcticus;* 33, *Campylobacter upsaliensis;* 34, *Campylobacter ureolyticus;* 35, *Campylobacter volucris.* +=all strains examined give a positive result. -=all strains examined give a negative result.<>=20–30 % strains grow at this temperature; []=50–60 % strains grow at this temperature; ()=76–93 % grow at these conditions; O2, aerobic conditions; mO2, microaerobic conditions; ANO2, anaerobic conditions; HmO2=microaerobic atmosphere enhanced with H2; F=7–27 % strains positive; V=29–57 % strains positive; M=70–95 % strains positive; *Weak growth.; †Biovar fecalis strains produce catalase; ‡Biovar paraureolyticus strains produce urease; §Urease-Positive Thermophilic Campylobacter (UPTC) variants.

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Table 3. Summary phenotypic data for extant *Helicobacter* and *Wolinella* spp.

Data are derived from original species descriptions [3, 19, 42, 44, 46, 57, 58, 62, 87, 121–154] (cf. Table S1) and/or On *et al.* [17].

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Growth temperature range (°C)	(30), 37, <42>	37–42	37–42	37	37	37–42	37–42	37–42	<30>, 37–42	37–42	37–42	37–42	37–42	37	37	[30], 37, (42)	37	37
Atmospheric requirements	mO2	mO2	mO2	mO2, CO2, ANO2*	mO2	mO2	mO2	mO2	mO2	mO2	mO2, ANO2	mO2	mO2, ANO2	mO2	mO2	mO2	ANO2	mO2, ANO2*
Oxidase	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Catalase	+	+	+	+	+	+	+	+	–	+	+	M	+	+	+	M	F	+
Nitrate reduction	–	–	–	+	+	+	–	V	–	–	+	+	+	+	+	–	+	+
Indoxyl acetate hydrolysis	–	+	+	–	–	+	+	+	+	–	–	F	–	–	+	+	–	–
Urease	+	+	+	+	+	+	–	–	–	+	–	–	–	–	+	–	–	+
Alkaline phosphatase	+	–	–	+	U	+	–	–	+	–	U	F	+	+	+	V	–	–
Hippuricase	–	U	U	–	–	–	U	U	–	U	U	–	–	–	–	–	–	+
Selenite reduction	–	U	U	U	U	–	U	U	–	U	U	–	U	U	–	–	–	U
Growth on: 2 % NaCl	–	U	–	–	–	–	U	–	–	U	–	–	–	–	–	–	–	–
1 % glycine	–	+	–	–	+	–	+	–	–	U	–	–	+	–	–	–	–	–
0.04 % TTC	–	U	U	U	+	–	U	–	V	U	U	+	U	U	–	+	+	U
TTC reduction	–	U	U	+†	U	+	U	–	V	U	U	+	U	–	–	+	+	+
Resistance to: Nalidixic acid (30 mg)	+	–	–	I	+	+	–	V	–	V	I	–	I	+	–	–	–	U
Cephalothin (30 mg)	–	+	+	+	+	–	+	+	F	+	+	+	+	+	–	–	+	U
Desirable features:																		
g-glutamyl transpeptidase	U	–	+	+	U	+	–	–	U	+	–	U	–	–	U	U	U	+
Growth on:																		
3.5 % NaCl	–	U	–	–	–	–	U	–	–	U	–	U	U	–	–	–	–	U
0.032 % methyl orange	F	U	U	U	U	–	U	+	–	U	U	+	U	U	–	V	M	U
0.1 % sodium fluoride	mO2	U	U	U	U	–	U	+	–	U	U	–	U	U	–	V	+	U
Anaerobic growth on 0.1 % TMAO	–	U	U	U	U	–	U	+	–	U	U	–	U	U	–	–	+	U

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Growth temperature range (°C)	37	30–42	37–42	37–42	37–42	37–42	37–42	37–42	37	37, (42)	37–42	37–42	(30), 37, <42>	37, [42]	37–42	37	37	37–42	37–42	37–42	37–42
Atmospheric requirements	mO2, ANO2	HmO2, ANO2	mO2	mO2	Mo2	mO2	mO2	mO2	mO2	mO2, (ANO2)	mO2, ANO2*	mO2, ANO2	mO2	mO2, ANO2	mO2	mO2, (ANO2)	mO2, ANO2*	mO2	mO2	mO2	ANO2
Oxidase	+	+	+	+	+	+	+	U	+	+	+	+	+	+	+	+	+	+	+	+	+
Catalase	+	+	+	+	+	+	+	+	+	+	+	M	+	+	+	+	+	+	+	+	+
Nitrate reduction	+	+	–	–	–	–	–	+	–	+	+	+	–	+	–	–	–	+	+	–	+
Indoxyl acetate hydrolysis	+	–	+	–	+	–	–	U	–	+	–	–	F	–	–	F	–	U	–	–	–
Urease	+	–	+	–	–	+	+	–	+	+	–	–	M	–	–	+	+	+	–	V	–
Alkaline phosphatase	U	+	–	–	–	+	–	+	–	+	+	–	+	–	–	V	+	F	–	–	–

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Table 3. cont.

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Hippuricase	–	–	U	U	U	U	U	–	–	–	–	–	–	–	U	–	–	–	–	–	–
Selenite reduction	U	U	U	U	U	U	U	U	–	+	U	+	–	U	U	–	U	U	U	U	+
Growth on: 2 % NaCl	U	–	U	U	U	U	U	–	–	–	U	–	–	U	U	–	-[a]	–	-[a]	U	+
1 % glycine	+	–	+	–	+	+	+	–	–	–	+	–	–	+	+	–	–	–	+	+	–
0.04 % TTC	+	U	U	U	U	U	U	–	–	+	U	V	V	U	U	–	U	U	U	U	–
TTC reduction	U	–	U	U	U	U	U	–	–	+	U	V	V	U	U	–	+	U	U	–	–
Resistance to: Nalidixic acid (30 mg)	+	–	–	+	+	+	+	–	–	–	–	+	M	+	+	–	U	+	–	V	–
Cephalothin (30 mg)	+	+	+	+	+	+	+	+	–	+	+	–	F	+	+	V	U	+	+	+	–
Desirable features:																					
g-glutamyl transpeptidase	U	+	–	–	–	–	–	–	U	U	U	U	U	–	+	+	+	+	–	–	U
Growth on:																					
3.5 % NaCl	U	U	U	U	U	U	U	–	–	–	–	–	–	U	U	–	-[a]	-[a]	-[a]	U	–
0.032 % methyl orange	U	U	U	U	U	U	U	U	–	–	U	+	–	U	U	–	–	U	U	U	+
0.1 % sodium fluoride	U	U	U	U	U	U	U	U	–	+	U	–	+	U	U	V	–	U	U	U	+
Anaerobic growth on 0.1 % TMAO	+	U	U	U	U	U	U	U	–	–	U	–	F	U	U	V	–	U	U	U	+

1, *Helicobacter acinonychis;* 2, *Helicobacter anseris;* 3, *Helicobacter aurati;* 4, *Helicobacter baculiformis;* 5, *Helicobacter bilis;* 6, *Helicobacter bizzozeronii;* 7, *Helicobacter brantae;* 8, *Helicobacter Canadensis;* 9, *Helicobacter canis;* 10, *Helicobacter cetorum;* 11, *Helicobacter cholecystus;* 12, *Helicobacter cinaedi;* 13, *Helicobacter cynogastricus;* 14, *Helicobacter equorum;* 15, *Helicobacter felis;* 16, *Helicobacter fennelliae;* 17, *Helicobacter ganmani;* 18, *Helicobacter heilmannii;* 19, *Helicobacter hepaticus;* 20, *Helicobacter himalayensis;* 21, *Helicobacter jaachi;* 22, *Helicobacter japonicus;* 23, *Helicobacter macacae;* 24, *Helicobacter marmotae;* 25, *Helicobacter mastomyrinus;* 26, *Helicobacter mesocricetorum;* 27, *Helicobacter muridarum;* 28, *Helicobacter mustelae;* 29, *Helicobacter pametensis;* 30, *Helicobacter pullorum;* 31, *Helicobacter pylori;* 32, *Helicobacter rodentium;* 33, *Helicobacter saguini;* 34, *Helicobacter salomonis;* 35, *Helicobacter suis;* 36, *Helicobacter trogontum;* 37, *Helicobacter typhlonius;* 38, *Helicobacter valdiviensis;* 39, *Wolinella succinogenes.* +=all strains examined give a positive result. -=all strains examined give a negative result. O2, aerobic conditions; mO2, microaerobic conditions; ANO2, anaerobic conditions. <>=18–27 % strains positive; ()=33–67 strains positive; []=77–92 % strains positive; F=6–29 % strains positive; V=33–58 % strains positive; M=83–93 % strains positive; *, Weak growth; †, when API method used; I, intermediate resistance; a, assumed; no growth on 1.5 % NaCl media.

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Table 4. Exemplar results of whole-genome comparisons for well-characterized strains of *Campylobacter*, *Arcobacter* and *Helicobacter* using Average Nucleotide Identity (ANI) [65] and Genome Blast Distance Phylogeny (GBDP) [66]

Genomes were accessed from public databases and ANI and GBDP values calculated using online tools (http://enve-omics.ce.gatech.edu/ani/ and http://ggdc.dsmz.de respectively) during December 2016. For ANI, values ≥95 were proposed to mimic conventional DDH results of ≥70 % [65]. For GBDP, values are proposed equivalent to conventional DDH [66]. Genome designations are GenBank reference numbers. The identity of non-type strain genomes was further verified by determining the phylogenetic relationship of their 16S rRNA gene sequences with those derived from type strains (Fig. 1 and Table S1). For *C. jejuni* subspecies, *C. coli*, *C. fetus* and *C. hyointestinalis*, MLST [155–157] was also undertaken. ANI, Average Nucleotide Identity; GBDP, Genome Blast Distance Phylogeny; SD, standard deviation; NCTC, National Collection of Type Cultures, England; CVM, Center for Veterinary Medicine, Maryland, USA; LMG, Laboratorie Microbiologie Ghent, Belgium; RM, Robert Mandrell collection, US Department of Agriculture; ATCC, American Type Culture Collection. T, type strain.

	Comparator			ANI Outputs*			GBDP outputs*		
Reference taxon/strain/genome	Taxon	Strain no.	Genome	Two way ANI	SD	No. of fragments	Formula 1	Formula 2	Formula 3
Campylobacter jejuni subsp. *jejuni* NCTC 11168/AL111168.1	*C. jejuni* subsp. *jejuni*	81116	NC_009839.1	97.83	1.81	6804	89.3	79.9	90.5
	C. jejuni subsp. *jejuni*	81-176	NC_008787.1	98.08	2.09	7029	93.9	81.6	94.3
	C. jejuni subsp. *doylei*	L269.97	NC_009707.1	95.97	2.3	6387	75.2	67	76.3
	C. coli	15-537360	NC_022660.1	85.18	6.84	4191	73.1*	27.9	58.7
	C. coli	CVM N29710	NC_022347.1	84.92	6.65	4142	75.5*	27.5	59.9
C. coli/15-537360/NC_022660.1	*C. coli*	CVM N29710	NC_022347.1	99.05	2.38	7593	97.6	89.1	97.9
C. fetus subsp. *venerealis*/84-112/NZ_HG004426.1	*C. fetus* subsp. *testudinum*	03-427^T	NC_022759.1	91.32	2.97	7293	86.6	46.6*	79.7
	C. fetus subsp. *fetus*	82-40	NC_008599.1	99.8	1.03	8390	94.5	97.3	96.6
	C. fetus subsp. *venerealis* bv. Intermedius	cfvi03/293	CP006999.2	99.87	1.28	8908	98.8	97.4	99.3
	C. hyointestinalis subsp. *hyointestinalis*	LMG 9260	NZ_CP015575.1	82.26	6.82	2223	34.4	22.1	30.1
	C. hyointestinalis subsp. *lawsonii*	LMG 15993	NZ_CP015576.1	80.77	6.22	2013	28.9	21.6	26.2
C. hyointestinalis subsp. *hyointestinalis*/LMG 9260 / NZ_CP015575.1	*C. hyointestinalis* subsp. *lawsonii*	LMG 15993	NZ_CP015576.1	94.65*	3.16	5862	70	57.6‡	69.5
Arcobacter nitrofigilis / DSM 7299^T/CP001999.1	*A. butzleri*	RM4018	NC_009850.1	78.09	4.7	1555	17.5	19.7	17.2
H. pylori / 26695 / NC_000915.1	*H. pylori*	Shi470	NC_010698.2	94.38*	2.59	6303	91.5	56.4*	87.3
	H. pylori	India7	NC_017372.1	94.85*	2.36	6580	91.4	59.4*	88.1
	H. pylori	SouthAfrica7	NC_017361.1	90.52*	3.16	5815	85.5	42.6*	77
	H. pylori	J99	NC_000921.1	93.65*	2.44	6360	92.1	54*	87.1
	H. mustelae	NCTC 12198^T	NC_013949.1	Insufficient hits		48	12.7	28.5	13.1
	H. hepaticus	ATCC 51449	NC_004917.1	Insufficient hits		27	12.7	19.8	13.1
	H. felis	ATCC 49179^T	NC_014810.2	76.97	8.29	69	12.8	19.7	13.2
	H. cinaedi	CCUG 18818^T	NC_020555.1	Insufficient hits		39	12.6	28.6	13
H. cinaedi / CCUG 18818^T / NC_020555.1	*H. canis*	NCTC 12740	NZ_KI669458	83.78	8.63	285	14	26.2	14.3
	H. hepaticus	ATCC 51449	NC_004917.1	77.94	4.84	1126	17.7	19.8	17.4

*Denotes results that are discordant with current classifications.

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with which a close phylogenetic relationship has been indicated, to determine interspecific genomic relatedness. Computational approaches described include Average Nucleotide Identity (ANI: [65]) and Genome Blast Distance Phylogeny (GBDP: [66]). Each algorithm is available online (presently http://enve-omics.ce.gatech.edu/ani/ for ANI: and http://ggdc.dsmz.de for GBDP). For new species proposals, we recommend both these analyses be presented where whole-genome sequences are used as the source of the genomic data. Complete or draft sequences of appropriate comparator type strains should be used as the basis for comparison. Table 4 lists comparisons between selected complete genomes of well-characterised members of the families *Campylobacteraceae* and *Helicobacteraceae*, using the default parameters suggested online for ANI and GBDP algorithms as exemplar output. These data identify some discordance between certain comparator taxa among almost all outputs and presently-accepted classifications; Formula 3 used for GBDP analysis performed optimally on this data set (Table 4). Nonetheless, a continued validation of Formula 3 for GBDP analysis is prudent.

Description of subspecies

There is precedent for the description of genetically- defined subspecies among the *Campylobacteraceae* in particular (notably for *C. jejuni, C. lari, C. fetus* and *C. hyointestinalis)* [31, 67–69]. Most of these subspecies (apart from *C. fetus* subsp. *fetus* and *C. fetus* subsp. *venerealis,* where the definition is historically based on differing disease aetiologies) [5, 31] are characterized by a high level of infraspecific similarity and distinctive phenotype and often ecotype. This definition aligns with the concept described by Wayne *et al.* [54], whereby 'subspecies designations can be used for genetically-close organisms that diverge in phenotype'. Subspecies should therefore exhibit DNA–DNA relatedness to the type strain of the species approximating or exceeding 70 %, with strains belonging to a given subspecies demonstrating a higher degree of genomic similarity, and clear differential characteristics in genotype, phenotype and/or ecotype between differing subspecies, as with the examples listed above.

Ecology

The natural habitat(s) of the proposed species should be detailed as much as possible, to include location(s), host species (if applicable), site of isolation, pathogenicity and clinical features (if appropriate).

Closing remarks

Minimal standards for describing new prokaryotic species aim to provide clear guidelines to the scientific community to assist in the delineation of novel taxa in a robust and unambiguous manner. This can only help the community at large who may be required to rapidly recognize emerging threats (or benefits) to public, plant, animal or environmental health. The standards described herein consider (i) previous recommendations for these taxa [8, 13, 14]; (ii) current, and indeed previous recommendations for characterisation of prokaryotes for taxonomic purposes [54–56], and (iii) the emerging discipline of genomic taxonomy, which is in a relative state of infancy and indeed flux [70–73]. At present, the continued need for a polyphasic taxonomic approach to achieve stable and robust classifications remains critical. These standards support that need.

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Conflicts of interest
The authors declare that there are no conflicts of interest.

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